

# Function of Labial Spines, Composition of Diet, and Size of Certain Marine Gastropods

BY

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(2 Text figures)

## INTRODUCTION

THE MORPHOLOGICAL BASIS of prey capture and penetration in many predatory marine prosobranch gastropods is fairly well documented: shell drilling by radular action and accessory boring organ (CARRIKER, 1955, 1961), harpooning with poisonous barbs (KOHN, 1959), and the use of the shell margin as a wedge (PAINE, 1962; WELLS, 1958b). It is surprising that little is understood of the functional significance of the most conspicuous external trait of apparent use in feeding: the single spine or labial tooth on the outer margin of the shell lip characterizing certain species in the Thaididae, Muricidae and Fascioliidae. Generalizations in the literature, apparently unsupported by data, state that the spine is thrust between the prey's valves, preventing closure and hence facilitating consumption by the predator (MACGINITIE & MACGINITIE, 1949). The data given below suggest that this generalization, while possibly correct in some instances, does not appear to hold for those species with the most conspicuous spines. An understanding of spine function is closely related to the effects that organism size and behavioral capabilities have on food consumption. Field data on both intra- and inter-specific dietary variations have been assembled to provide a basis for comparisons of different spine-bearing species.

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## Specific Use of the Spine

Direct observations of spine use in the natural setting are difficult and tedious to make, and most of the present conclusions are based on inference, though wherever possible, supported by laboratory observation.

### *Acanthina brevidentata* (Wood, 1828)

This species, on the basis of 80 observations at two stations on the Pacific coast of Costa Rica, was seen to feed mainly (75%) on *Chthamalus* sp., although small individuals of other barnacle species may well be consumed. The remainder of the observed diet consisted of small mussels. The spine is well formed, though relatively short, being about 1 mm in length in individuals 2 cm long. The snail penetrates barnacles by drilling between their opercular plates. No evidence was obtained for spine use, although both drilling and prying the prey open with the spine would be redundant acts.

### *Acanthina tuberculata* (SOWERBY, 1835).

Despite the local abundance and large size (to 6-7 cm) of this intertidal species in the upper Gulf of California, I have rarely found it feeding. The spine is short (1-2 mm), often just a fold in the margin. In eight of fourteen feeding observations (57%) the carnivorous gastropod *Acanthina angelica* was the prey. There was no evidence of shell drilling in these prey; rather parts of the prey's operculum appeared to have been rasped away. In four instances limpets, *Crucibulum* sp., were being consumed. Again there was no evidence of drilling but in these cases the outer margin of the prey's shell had been shattered, probably by the *Acanthina's* shell. Casual observations on a 6 cm individual maintained in captivity for over 2 years indicate no deviation from the field pattern: operculate gastropods seem to be the preferred food of a variety offered, and are penetrated by having a corner of their operculum rasped away while being held in the *A. tuber-*

*culata*'s foot. I have never obtained any evidence that large individuals can drill, or that the spine is used. In fact, most gastropod prey withdraw so deeply into their shells that the short labial spine would be functionless.

*Acanthina angelica* (I. OLDROYD, 1918).

This species is widely distributed in the upper Gulf of California in intertidal waters (KEEN, 1958), and I have observed it at San Felipe, Puertocitos, and Puerto Peñasco. All observations to date suggest that it is a barnacle "specialist"; of 432 records of prey only two non-barnacles (both 10 mm individuals of the gastropod *Cerithium stercusmuscarum* VALENCIENNES, 1833) have been found. I have no data to indicate any strong prey preference being exercised within the abbreviated spectrum usually consumed, as is true for *Thais lapillus* (LINNAEUS, 1767) (CONNELL, 1961). For instance, at San Felipe in March, 1963 *Acanthina angelica* was observed eating the barnacles *Chthamalus* sp., *Tetracita squamosa*, and *Balanus amphitrite*. These barnacles occupy recognizable zones and an estimate was obtained of the percent of *Acanthina* feeding in each area. There was no difference in feeding intensity where *Chthamalus* and *Balanus*, both small species, were abundant, 14/26 (54%) and 28/45 (62%) respectively of *Acanthina* picked at random actually feeding. On the other hand, only 48/120 (40%) of the individuals adjacent to *Tetracita* were feeding. The reduced incidence may reflect some greater difficulty in penetrating these larger, thicker shelled, barnacles, but say little about food preference, since if the reward to the predator in terms of nourishment attained per unit time was greater, as might be expected from much larger prey, *Tetracita* would be the optimal food.

In every instance the prey were being drilled, and characteristic holes were noted between the barnacles' opercular valves or in their lateral plates. Although *Acanthina* was observed during all stages of the feeding process, no function was noted for the apertural spine.

Another *Acanthina angelica* population was observed in March, 1964, at Puerto Peñasco, Mexico, on the opposite shore of the Gulf from San Felipe. The basic environmental situation appeared quite similar except that *Acanthina* appeared to be polymorphic for spine length. The majority of individuals were characterized by short (3 mm or less) spines and were eating *Chthamalus*. A number, however, characterized by immense (6-10 mm) spines were devouring *Tetracita*, and it is from these latter individuals that a definite indication of the spine's function was obtained. Notice that all logical relationships between where the hole was drilled and the spine's position were encountered, although in far from equal frequency (Table 1). These data indicate that in only about

35% of the observations was the spine actually inside the opercular cavity of the barnacle, and that only 25% of the snails were feeding through the opercular plates. In the remaining instances both the spine and the point of active drilling were removed from the barnacle's natural opening. Five examples were noted (not recorded in Table 1) in which the spine was hooked around or in one barnacle, and the snail was feeding or drilling on a second. The conclusion seems inescapable that in these large-spined individuals the spine is used for purchase and is not directly involved in penetrating the prey.

Table 1

The relationship between spine position and hole position in a population of long-spined *Acanthina angelica* feeding on *Tetracita squamosa*.

	Position of spine		Totals
	Inside opercular opening	Outside opercular opening	
Where barnacle was drilled	Outside opercular opening	8 30	38
	Inside opercular opening	10 4	14
	Totals	18 34	52

Twenty to thirty short-spined individuals from the upper Gulf have been maintained at Seattle, Washington, and laboratory observation obtained. After a varied period of starvation, these were offered *Balanus glandula* and the ensuing events were studied. The snails invariably spent some time orienting themselves on the barnacles. Then the spine, located between the eyes of a crawling snail, was hooked over the outside rim of the barnacle or in some convenient cranny, after which the barnacle was drilled. Although data were obtained from 15 different individuals, little variation in this procedure was noted, and never was the spine forcibly thrust between the prey's opercular plates. Seemingly the spine, as in the larger individuals, is used solely for purchase.

Spine length is quite labile in this species and varies from area to area. The relationship between shell length and spine length is compared in Figure 1 for the two most different populations yet examined and a third characterized by the longest spines. The former two

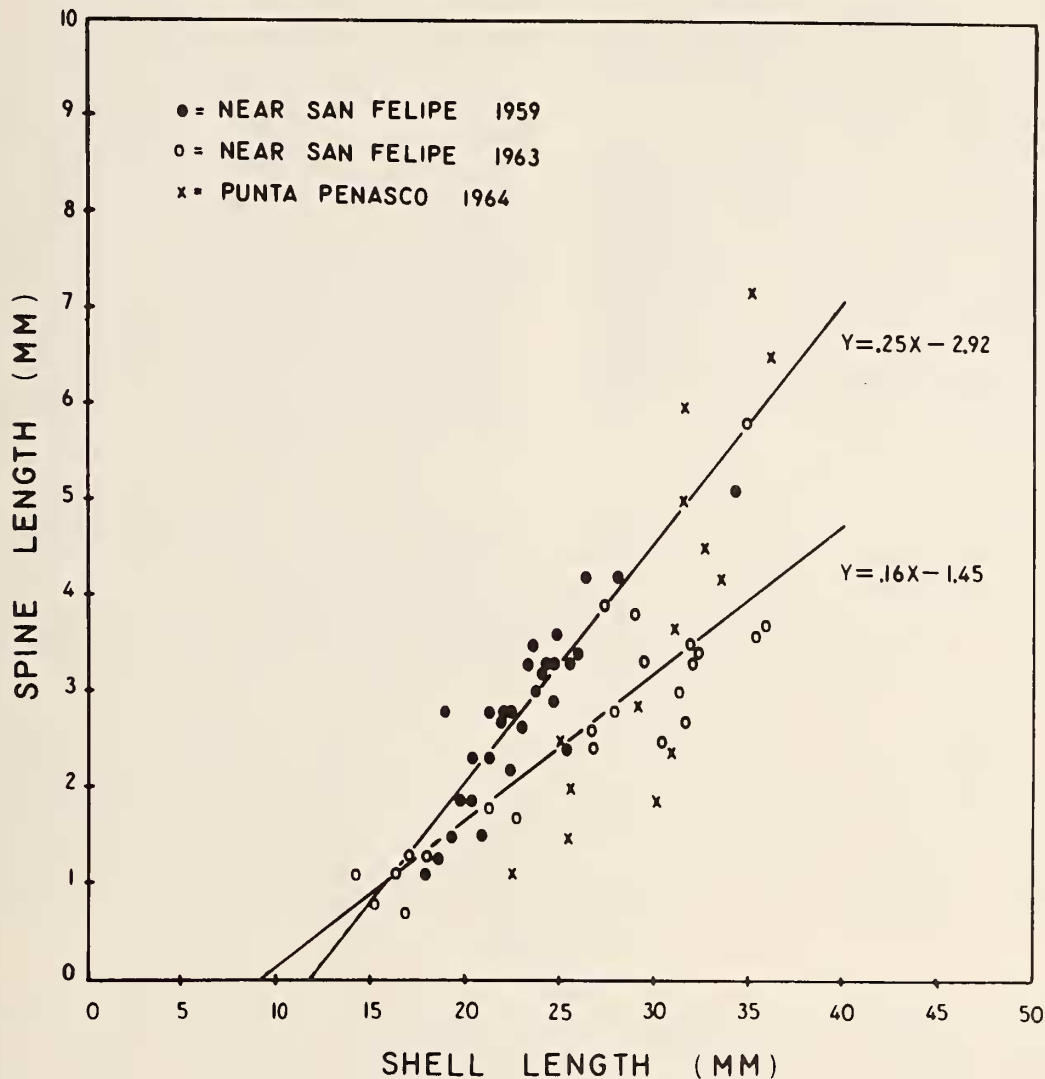


Figure 1

Spine-shell length relationships of three populations of *Acanthina angelica*.  
The significantly different regression lines were fit by least squares.

samples were collected approximately 30 miles south of San Felipe by Dr. R. Stohler. Regression lines fit by least squares indicate significantly different relationships between shell length and spine length within a local area, but sampled four years apart. Such would occur if spine length varied in response to barnacle size, and the barnacle species composition had changed gradually in this local area from 1959 to 1963. Both curves have similar

origins, reflecting the shell length at which the spine can be measured. The situation at Puerto Peñasco is rather different. Inspection of Figure 1 suggests a curvilinear relationship between the variables. However, the few points could also be interpreted as a composite of two linear relationships, one from approximately 10 to 30 mm shell length, the other from 30 to 37 mm. It is tempting to suggest that the shorter spined individuals were probably



eating small barnacles while the longer spined ones were consuming mature *Tetraclita*. Further field data are needed to resolve the reality of such a polymorphism.

*Opeatostoma pseudodon* (BURROWS, 1815)

KEEN (1958, p. 416) has stated that this member of the Fascioliidae has "... perhaps the longest apertural tooth developed by any gastropod," and of the species for which I have data, this assertion is borne out by high spine-shell length ratios. For instance, a shell 40 mm long may bear a 14 mm spine. My observations were all made at El Coco Beach on the Pacific coast of Costa Rica in July, 1964, where *Opeatostoma* was found living under rocks semi-buried in coral sand. Observations suggest it to be active nocturnally.

The species seems to be mainly verminivorous, although other items may well be eaten. In an examination of about 85 individuals during daylight hours, only 3 were found feeding. One of these was definitely consuming a serpulid polychaete. The remaining two were both firmly anchored in the sandy substrate by their immense spines, apparently feeding on "sand tubes," although no worm remnants were observed. Nocturnal observations added three more instances of feeding on tubicolous polychaetes plus one example of a small bivalve being taken.

In the cases of positively observed feeding, there was no indication that the spine had ever been brought directly to bear on the prey, and in fact, the spine's length (up to 15 mm) would mitigate against this. I feel that the spine

Table 2

New and literature accounts of size-feeding relationships of the Fascioliidae.

(G) indicates gastropod prey; (B), bivalve prey.

PAINE (1963) gives a breakdown to species of the categories listed.

Species	Adult length (cm)	Natural diet	% of total diet in category	Number of observations	Source
<i>Fusinus</i> spp.	4	polychaetes	100	11	this paper
* <i>Opeatostoma pseudodon</i> (BURROWS)	4.8	polychaetes small bivalves	86 14	7	this paper
<i>Fasciolaria hunteria</i> (PERRY)	8	polychaetes gastropods small bivalves carriion	41 13 32 13	76	PAINE, 1963
<i>Pleuroploca</i> ( <i>Fasciolaria</i> ) <i>filamentosa</i> (RÖDING)	10	<i>Calliostoma</i> (G) and a <i>murex</i> (G)		2	RISBEC, 1932
<i>Pleuroploca</i> ( <i>Fasciolaria</i> ) <i>trapezum</i> LINNAEUS	13	<i>Margaritifera</i> (B)			fide GRAHAM, 1954
<i>Fasciolaria tulipa</i> LINNAEUS	17	bivalves large gastropods carriion <i>Strombus</i> (G)	25 67 8	52	PAINE, 1963
				frequent	ROBERTSON, 1961 RANDALL, 1964
<i>Fasciolaria princeps</i> SOWERBY	23 - 30	<i>Hexaplex</i> (G)			SORENSEN, 1943
<i>Pleuroploca gigantea</i> KIENER	35	bivalves large gastropods <i>Melongena</i> (G)	20 80	66	PAINE, 1963
					HATHAWAY & WOODBURN, 1961

\* spine bearing species

functions in anchoring the animal to the coral rubble substrate, and is not directly involved in prey penetration.

### Size and Diet

The basic fact that, other things being equal, larger organisms need more energy for maintenance, is expressed at both inter- and intra-specific levels when dietary comparisons are made.

The Fascioliidae are carnivorous gastropods lacking any drilling apparatus, which penetrate prey by forcefully inserting the proboscis into the prey, often accompanied by mild rasping with the radula or use of the shell margin (WELLS, 1958a; PAINE, 1963). The family is well suited for studies on size-diet relationships because it includes *Pleuroploca gigantea* (KIENER) reputed to be the largest living carnivorous gastropod. Table 2 summarizes all available comparisons of size and diet. The *Fusus*, observed near Puertocitos, consumed small serpulids by inserting the proboscis down the worm tube, a food-getting stratagem also characterizing *Fasciolaria hunteria* (PAINE, 1963). The observations on *Opeatostoma* indicated that tubicolous worms were its principal prey. In the 6 larger species the diet is composed of either bivalves or gastropods and no worms are consumed. In the Fascioliidae, then, smaller species eat polychaetes, and an increasing reliance on bivalves and gastropods, both more substantial food items, occurs with increasing size.

Similar interspecific trends characterize the Thaididae and Muricidae, considered jointly in Table 3 because of their close taxonomic position and common possession of a shell-boring mechanism. These data include only my

observations from the Pacific coast of Costa Rica (*Acanthina brevidentata*, *Thais kiosquiformis* (DUCLOS, 1832), *Thais biserialis* (BLAINVILLE, 1832), *Thais melones* (DUCLOS, 1832)) and the northern end of the Gulf of California (the remaining species named in Table 3). The general impression that the smaller species are barnacle specialists, or at least eat few other gastropods, would be supported by the work of CONNELL (1961) on other *Thais* species, and HEWATT (1934) on *Acanthina* sp. The very high percentage of gastropods in *A. tuberculata*'s diet may be due to relatively few observations on mainly large individuals, or may fairly indicate the high degree to which this species preys on *A. angelica*. The differences between *Hexaplex* and *Muricanthus* in regard to the proportion of barnacles taken is due to subtle habitat differences: although they are often found together, small *Muricanthus* live in cobble patches wherein barnacles abound. When only adults of both species are considered there is no change in the *Hexaplex* data whereas for *Muricanthus* the barnacle feeding incidence drops to 0% and the percentage of gastropods rises to 43%.

Both the above size-diet correlations include the tacit assumption that a particular species' post-larval diet is a fixed entity. The assumption is partially false, gastropod diets being known to vary geographically (THOMPSON, 1964) and presumably also during post-larval development. Enough data are available to examine intraspecific dietary changes related to size increase only in *Muricanthus nigrinus* (PHILIPPI, 1845). Observations made near Puertocitos in March 1962 and 1963, although pooled in

Table 3

The relationship between adult shell length and the relative contribution of barnacles and gastropods to a species diet. The asterisk indicates a spine-bearing species.

Species	shell length (cm)	Number of observations	% barnacles	% gastropods
<i>Morula ferruginosa</i> (REEVE)	2.5	39	100	0
* <i>Acanthina brevidentata</i> (WOOD)	3.0	80	80	0
* <i>Acanthina angelica</i> OLDROYD	3.9	432	99	1
<i>Thais kiosquiformis</i> (DUCLOS)	4.3	84	100	0
<i>Thais melones</i> (DUCLOS)	4.8	17	0	17
<i>Pterynotus erinaceoides</i> (VALENCIENNES)	5.0	7	0	14
* <i>Acanthina tuberculata</i> (SOWERBY)	6.2	14	0	89
<i>Thais biserialis</i> (BLAINVILLE)	7.5	99	23	18
<i>Hexaplex erythrostomus</i> (SWAINSON)	10.0	63	0	23
<i>Muricanthus nigrinus</i> (PHILIPPI)	2.0 - 15.0	118	34	29
	6.0 - 15.0	20	0	43

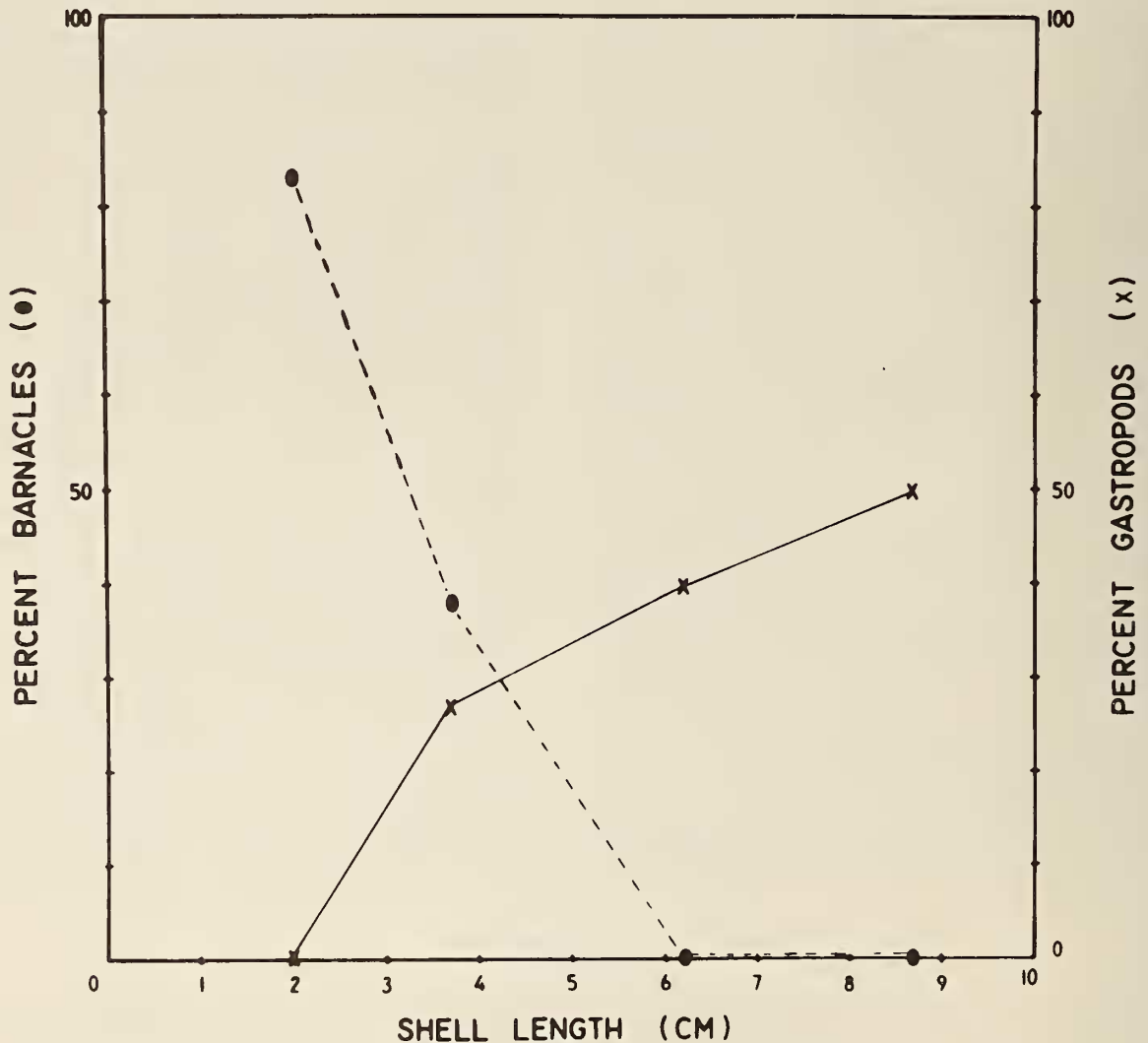


Figure 2

The changes in the relative frequency of barnacles (o) and gastropods (x) in the diet of *Muricanthus nigratus* with increasing size (= age).

Figure 2, show comparable trends when examined separately. There is a clear switch in diet with increased size, with the pattern being quite similar to that given in Table 3 for a haphazard collection of thaidids and muricids. Furthermore, inferences can be drawn about behavioral changes in the *modus operandi* of *Muricanthus* from observations on the prey at time of capture. Small *Muricanthus* drill barnacles, but with increasing size tend to use their shell lip to chip open prey. Some prey are still drilled, but at lengths greater than 5 cm shell use is

predominant. Thus, accompanying the ontogenetic change in diet is the acquisition of a new behavioral capacity not found in, or at least not used by, the smaller individuals.

#### Generalization and Conclusion

When the trophic capacities of varying species of gastropods are examined, a positive correlation between trophic position and an increased diversity of prey consumed may be found (PAINE, 1963). ELTON (1927) was apparently the first to recognize that these correlations with the pred-



ator's position were primarily due to an increasing relative scarcity of larger prey species which, in turn, tended to necessitate a more catholic diet if the predator's food requirements were to be met. This general tendency is clearly illustrated for adult members of the Muricidae and Thaididae (Table 3), in which increased shell length is accompanied by an apparently more diverse diet composed of larger prey organisms. The trend is clear in the Fascioliidae (Table 2) only if diversity is considered to be measured by the number of different higher taxa consumed. The proposition can be offered that these larger carnivorous gastropods are trophic generalists, within certain limits, attacking and consuming a greater variety of morphologically-different prey than do small species. In the Fascioliidae, small species use only the proboscis and larger ones both the proboscis and shell lip. In the Muricidae, small individuals drill while larger ones both drill and chip open their prey. Smaller species, eating a reduced variety of prey and probably characterized by fewer prey-penetrating mechanisms, may be called specialists.

Comparison of Tables 2 and 3 shows that those species with the longest spines, *Opeatostoma* and *Acanthina angelica* are of intermediate to small size, and both are specialists, one on worms, the other on barnacles. In both, the spine does not function directly in food gathering, but must have some adaptive function. In *A. angelica* I believe this to be the ability of snails with long spines to anchor themselves more firmly to the substrate while drilling. A firmer attachment could be maintained if the spine was inserted in a crevice, or barnacle opercular opening, and tension maintained against it, holding the snail more firmly to the surface. Since in intertidal communities large individual barnacles are usually zoned fairly high, and undoubtedly take longer to penetrate, a more secure "grip" on the prey would increase the probability of successful penetration by the predator without being dislodged, and would tend to minimize water loss on exposure to air.

The relative diminution or absence of spines in larger species may be considered a preadaptation, so to speak, foretelling the eventual abandonment of epifaunal sedentary prey. For instance, the short spine of the large species *Acanthina tuberculata* and *Murex fortispina* (FRANÇOIS, 1891), spines at best described as strengthened folds of the aperture, may be the result of potential feeding inefficiency associated with a large spine, when larger, specifically more diverse, prey are needed to meet the organism's nutritional requirements. Such prey usually must be dug (bivalves) or pursued (gastropods), acts in which a lengthy spine might prove detrimental.

In the context of the relationship of spine size, body length, and degree of dietary specialization within the Muricidae and Thaididae, there is a surprising degree of agreement between Figure 2 and Table 3 of the length at which gastropods begin to form a greater percentage of the diet than barnacles. In both the intra- and inter-specific comparisons this occurs at a shell length of 4-5 cm, suggesting some practical limit to the size at which energy expended in penetrating and devouring barnacles (or perhaps other small prey) is greater than the return for these efforts. Continued balanophagy or trophic specialization, then, above this size would be inefficient, and a switch in dietary emphasis appropriate to the general situation would be expected. The ecological consequences of these dietary changes, demonstrated for *Muricanthus*, cannot yet be explored since data on the diet of small individuals of most large species are unavailable. It seems clear that in *Muricanthus*, and generally in the Fascioliidae, Thaididae, and Muricidae, attainment of large size is accompanied by a switch in trophic position from that of a secondary consumer to higher status. What role this plays in the organization and stabilization of marine communities is unknown.

## SUMMARY

A combination of literature data with new observations indicates the reality of the expected correlation of both the diversity of, and general size of, prey with increasing body size within the gastropod families Fascioliidae, Muricidae and Thaididae. In the species *Muricanthus nigritus* the composition of the diet changes at a shell length of 4-5 cm from one in which barnacles have predominated, to one characterized by gastropods. A comparable switch characterizes the Muricidae and Thaididae, suggesting that specialization on small prey is only profitable energetically when the predator itself is small. Gastropods with a labial spine appear to be feeding specialists. The spine itself does not appear to function in prey penetration, but rather in anchoring the predator to the substrate.

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